

Structure and Phylogenetic Significance of *Diabolichthys speratus* gen. et sp. nov., a new Dipnoan-like Form from the Lower Devonian of Eastern Yunnan, China

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A new dipnoan-like form found in association with *Youngolepis* from the Lower Devonian of eastern Yunnan, China, is described as *Diabolichthys speratus*, gen. et sp. nov. The morphological account covers the dermal skull roof, ventral view of anterior cranial portion, detached pterygoid plates and lower jaw rami. The new form is compared with *Youngolepis*, with previously-described dipnoans, and with other osteichthyans. Analysis of character distribution suggests that *Diabolichthys* is more closely related to dipnoans than to other fishes, and forms the sister-group of all previously described dipnoans. Unique features exhibited by this new form (e.g. skull roof pattern, palatal and lower jaw structure and related palatal bite, position of posterior external nasal opening at the mouth margin lateral to the premaxillary, reduced and attenuated posterior sector of the premaxillary) have possible significance for the current debates concerning the interrelationships of lobe-finned fishes and the origin of tetrapods.

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INTRODUCTION

Some remarkable dipnoan-like specimens associated with *Youngolepis* (Chang and Yu, 1981; Chang, 1982) were discovered by the junior author in 1980-1981 in the Qujing district, eastern Yunnan, China. The material includes two fairly complete skulls, five anterior cranial portions (some complete and some not), five fragmentary (?pterygoid) tooth plates, two right lower jaw rami and one left prearticular. This material is described and compared with previously known dipnoans (Denison, 1968, 1968a; Miles, 1977; Thomson and Campbell, 1971), with *Youngolepis* and *Powichthys* (Jessen, 1975, 1980) and with other sarcopterygians including the problematical 'rhipidistians' (Jarvik, 1942, 1966, 1972, 1980; Rosen *et al.*, 1981; etc.). As the present material is remarkably distinct from all other known forms, a new genus and species, *Diabolichthys speratus*, is hereby erected. Analysis of character distribution suggests that this new form is more closely related to dipnoans than to other osteichthyans and that it constitutes the sister-group of all previously described dipnoans (cf. Miles, 1977: 306, fig. 157).

This new form occurs in the same argillaceous limestone as *Youngolepis* and its age is either Gedinnian, or late Gedinnian to early Siegenian (Li and Cai, 1978). A brief account of the associated fauna and the geological setting can be found in Chang (1982). The present material is earlier in occurrence than the early or possibly middle Siegenian *Uranolophus wyomingensis* (Denison, 1968), which constitutes the earliest dipnoan record so far known. Dipnoan material previously reported from China consists only of a Middle Devonian tooth plate from Yunnan (Wang, 1981) and the

Mesozoic ceratodontid tooth plates from Sichuan (Liu and Yeh, 1957). *Diabolichthys* described in this paper is better preserved and provides more cranial details for morphological and phylogenetic studies. As this new form is generally similar to the associated *Youngolepis* whose braincase and other cranial structures have been studied by the serial grinding method (Chang, 1982), comparison tended to be made with *Youngolepis* during initial observations. However, the necessity to specify synapomorphies at proper levels has always been kept in mind to reduce the risk of circular phylogenetic arguments. While the present paper tries to suggest an explicit phylogenetic scheme involving *Diabolichthys*, previously known dipnoans, *Youngolepis*, *Powichthys* and some 'rhipidistians', even a tentative scheme is limited by the problematical status of 'rhipidistians' and by many other unsettled problems of morphology and taxonomy. Preparations are under way to make serial grinding sections to provide additional information on the internal cranial structures of *D. speratus*, and the hypothesis suggested in this paper is obviously tentative pending this study.

DESCRIPTION AND COMPARISON

Diabolichthys gen. nov.

Diagnosis: Dermal skull roof with anterior portion relatively long; 'parietals' or I-bones anteriorly separated from each other by median element or B-bone but posteriorly meeting each other in midline; J-bones separated from each other by B-bone and other median elements; snout fairly short and orbit anteriorly positioned, with long intertemporal-supratemporal series (X, Y₁ and Y₂ bones) at skull roof margin; no pineal opening; premaxillary independent; anterior and posterior nasal openings at mouth margin; premaxillary with no marginal teeth but further inward low-crowned teeth forming continuous patch with vomerine teeth; posterior sector or premaxillary thin and narrow; pterygoid and prearticular tooth plate-like, covered with flattened teeth in regular rows; parasphenoid extending forward to vomers and pterygoids not meeting in midline; endocranium deep and narrow and palatoquadrate not fused with endocranium; buccohypophysial opening present; rostral tubuli present in endoskeletal part of snout.

Etymology: diabolus (Latin) = devil; ichthys (Greek) = fish.

Type species: *Diabolichthys speratus* sp. nov.

Diabolichthys speratus sp. nov.

Diagnosis: see genus diagnosis.

Etymology: speratus (Latin) = to have hope.

Holotype: V7238, I.V.P.P. Beijing.

Locality and Horizon: Xichong., Qujing district, eastern Yunnan, China: Xitun Member, Cuifengshan Formation (Lower Devonian).

Dermal skull roof: Dermal skull roof bears general similarity to *Youngolepis* (Chang, 1982). No pineal opening exists, although a corresponding elevation on skull roof surface indicates that the pineal body is rather anteriorly positioned. In specimen V7237, the skull roof is wider and shorter than in *Youngolepis*, the length of the skull (from its anterior tip to the posterior margin of the 'parietal' or I-bones) is 1.2 times its maximum width (the corresponding ratio in *Youngolepis* ranges from 1.3 to 1.6). In specimen 7238, the ratio is 1.3 and close to that in *Youngolepis*. However, this specimen is small with the skull roof only half as long as that of specimen V7237; it probably represents a juvenile. The posterior margin of the orbit is more posteriorly situated and the orbit is larger than in specimen V7237 or in *Youngolepis*. This is consistent with the usual observation that the orbit is relatively larger in juveniles than in adults.

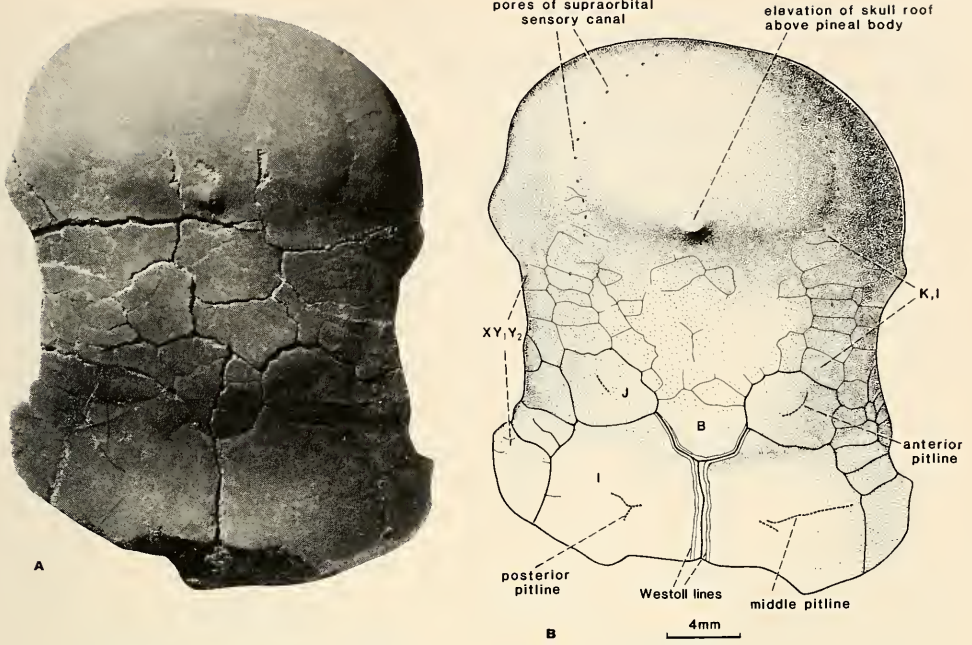
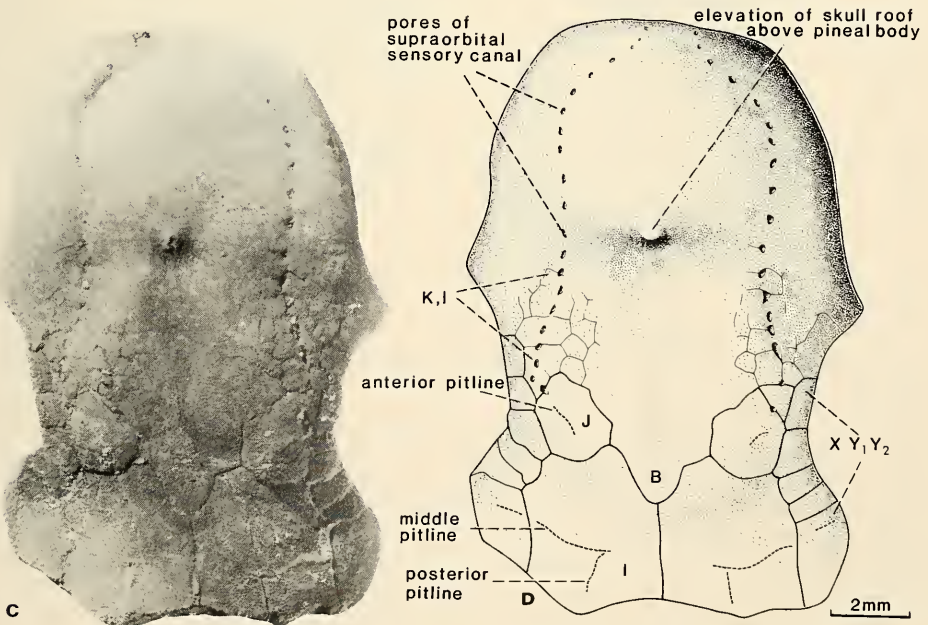


Fig. 1. *Diabolichthys speratus* gen. et sp. nov. Photographs and sketches of cranial roof in dorsal view. A, B, specimen V7237; C, D, V7238.



The skull roof elements corresponding to the parietals or the parietal shield of *Youngolepis* are much shorter while the portion anterior to the 'parietals' (I-bones in Fig. 1B, D) is much longer than in non-dipnoan osteichthyans; the ratio between the two portions in specimens V7237 and V7238 is 2.4:1 and 3:1 respectively, whereas the corresponding ratio in *Youngolepis* is 1.9:1. Even though the greater part of the 'parietals' still meet each other in the midline, they are anteriorly separated from each other by a median element (B-bone in Fig. 1B, D). The supraorbital sensory canal is rather long and its posterior sector is carried by a series of small bones. As noticed in specimen V7238, sutures between these small bones usually form the locations accommodating pores of this canal. The lateral margin of the skull roof is formed by another series of small plates (X, Y₁ and Y₂-bones in Fig. 1B, D). Among osteichthyans, the skull roof pattern revealed by this new form comes closer to that of primitive dipnoans than to that of actinopterygians or 'crossopterygians'. When compared with the skull roof pattern in Early Devonian dipnoans, such as *Dipnorhynchus lehmanni* (Lehmann and Westoll, 1952; Lehmann 1956), *Dipnorhynchus sussmilchi* (Thomson and Campbell, 1971) and the North American *Uranolophus wyomingensis* (Denison, 1968, 1968a), the new material from Yunnan reveals the following points of correspondence. The 'parietals' or I-bones are similarly positioned and carry pit-lines corresponding to the middle and posterior pit-lines in dipnoans or the transverse and posterior oblique pit-lines in *Youngolepis* (according to Jarvik's terminology). Anterior to the I-bones lie the well-delineated J-bones, bearing pit-lines corresponding to the anterior pit-lines or the frontal pit-lines in *Youngolepis*. In specimen V7237, the posterior section or terminal point of the supraorbital sensory canal cannot be traced. In specimen V7238, the posterior-most pore-opening for this canal lies at the suture between the J-bone and the anteriorly adjoining element (Fig. 1D). It could be assumed that the posterior end of this canal extends backwards into the J-bone and this suggests a similar pattern to that of *Dipnorhynchus sussmilchi* where J carries both the posterior end of the supraorbital sensory canal and the anterior pit-line (cf. Thomson and Campbell, 1971: 26-27, fig. 6A). The median element anterior to the I-bones and lying between the J-bones partially corresponds to the B-bone. In specimen V7237, this element or B-bone is anteriorly delimited by traceable sutures marking out a mosaic of small and variable elements (Fig. 1B), whereas in specimen V7238 no traceable sutures exist to indicate the anterior margin of B. The small bones anterior to J and carrying the posterior section of the supraorbital sensory canal, probably correspond to the series including K and L-bones. Lateral to the I, J and K-bones, the small bone series at the lateral margin of the skull roof probably corresponds to the Y₁, Y₂ and X series.

Besides these similarities to primitive dipnoans, the Yunnan specimens manifest the following differences from later dipnoans: the snout and the nasal region are relatively short; the orbit and the pineal elevation are relatively anteriorly positioned; the I-bone and the marginal series corresponding to Y₁, Y₂ and X-series are long; and the I-bones meet each other along a considerable portion of their median margins (Fig. 1A, B, C, D).

Ventral view of anterior cranial portion: As in *Youngolepis* (Chang, 1982: 12), the premaxillary is an independent element and the anterior section of the infraorbital sensory canal and the ethmoidal commissural canal probably lie between the premaxillary and the posteriorly adjoining elements. The snout manifests a greater degree of downward and inward bending than that of *Youngolepis*, and consequently a considerable portion of the premaxillary lies inside the mouth cavity and bears no cosmine. However, the relative proportion of the premaxillary which remains outside the mouth cavity and bears cosmine varies with the degree of downward and inward

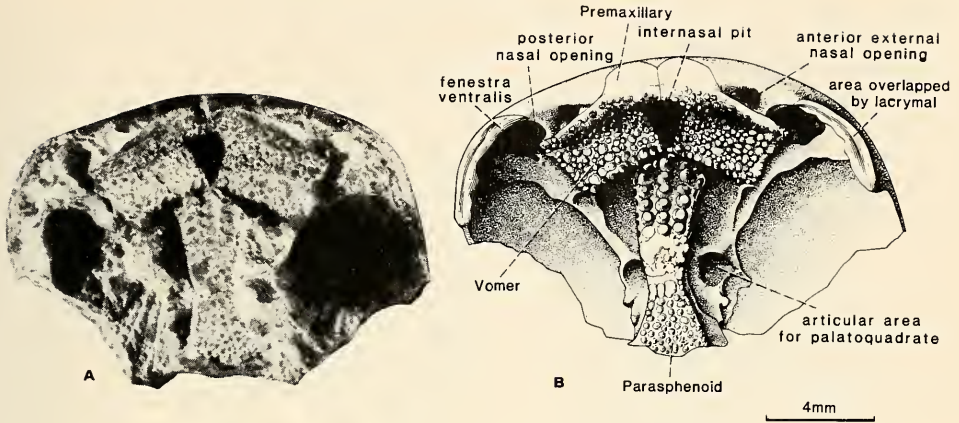
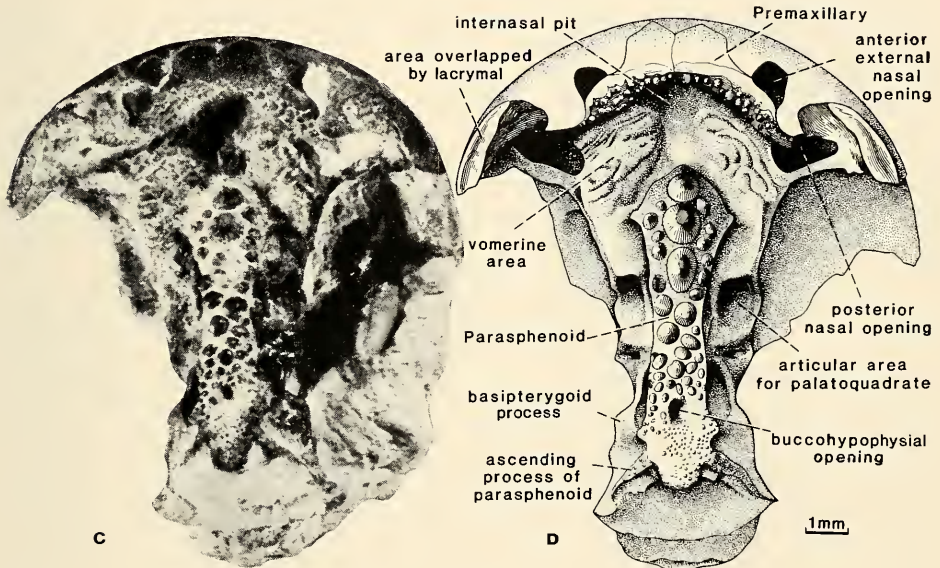


Fig. 2. *D. speratus* gen. et sp. nov. Photographs and sketches of anterior cranial division in ventral view. A, B, specimen V7239; C, D, V7240.



bending of the snout. In specimens V7239 and V7240, the portion remaining outside is relatively large, whereas in specimen V7237 it is relatively small. Unlike *Youngolepis*, the part of the premaxillary lying inside the mouth cavity is covered with low-crowned teeth and the mouth margin has no row of large teeth. The ventral portion of the original facial part (cf. pars facialis of Jarvik, 1942) of the anterior sector of the premaxillary, and the entire facial part of the posterior sector, face downward and inward and bear no cosmine at all. Thus the facial surface of the posterior sector of the premaxillary is fully (as in specimen V7239) or almost fully (as in specimen V7240) covered with low-crowned teeth manifesting traces of wear.

The vomer is rectangular in shape and covered with low-crowned teeth similar in

shape to those of the premaxillary. Anteriorly the vomerine tooth band merges with the downward and inward facing tooth band of the premaxillary and the two portions form a continuous tooth patch (Fig. 2A, B, C, D). All this indicates that the downward and inward facing portion of the anterior sector of the premaxillary and the entire posterior sector of the premaxillary are situated inside the mouth cavity. The possible occlusal relations may be inferred from the lower jaw tooth pattern described later in this paper. The premaxillary is thin and narrow at the posterior end and posteriorly does not reach to the level of the postnasal wall.

In specimens where the vomer is not preserved, the vomeral area has a rugged uneven surface divided by a network of grooves into raised areas of irregular shape and size, rather similar to those of *Youngolepis*. Between the vomeral areas, the ventral surface of the endocranium bears a shallow depression corresponding to the internasal pit in *Youngolepis* (Fig. 2C, D). In specimens with preserved vomers, a deep depression is formed between the vomers and the premaxillaries because the vomer is so deep (Fig. 2A, B).

The parasphenoid is long and narrow and extends anteriorly to the ventral side of the most posterior part of the ethmoidal region where it adjoins the vomer. The anterior part of the parasphenoid bears fairly large teeth while the posterior part bears small and irregular teeth which are also low-crowned and flattened. The anterior part of the toothed portion of the parasphenoid is flanked by deep dorsally extending wings, that give a trough-like appearance to the parasphenoid in the anterior two thirds of its total length. This trough accommodates the interorbital portion of the endocranium. The buccohypophysial opening lies in a depression in the posterior part of the parasphenoid. Posterior to the level of this opening, the parasphenoid has a short process extending laterally. More posteriorly, a fairly high ascending process extends dorso-laterally and abuts against the lateral wall of the endocranium at a level posterior to the basipterygoid process (Fig. 2C, D). The parasphenoid does not cover the ventral surface of the otico-occipital region.

The anterior external nasal opening lies precisely at the mouth margin. The posterior nasal opening agrees with that in *Youngolepis* in certain respects but differs in others. As in *Youngolepis*, specimens with no preserved vomers reveal a fairly large fenestra in the posterolateral portion of the floor of the nasal cavity and this fenestra is divided into medial and lateral portions by the posterior sector of the premaxillary (Fig. 2C, D). However, as in *Youngolepis*, specimens with preserved vomers show that the portion of the said fenestra lying medially to the premaxillary is covered ventrally by the vomer which forms part of the floor of the nasal cavity. Consequently, this fenestra has an outlet only through the portion lying laterally to the premaxillary, i.e., through the posterior external nasal opening (Fig. 2A, B). In *Youngolepis*, the premaxillary is fairly long and wide and bears a row of large teeth at the mouth margin. Beyond this tooth row, the entire facial (external) surface of the *Youngolepis* premaxillary is covered with cosmine and obviously the premaxillary and the posterior external nasal opening lateral to it are both situated outside the mouth cavity (Fig. 3). As distinct from *Youngolepis*, a considerable portion of the facial part of the premaxillary in the new form bears a broad band of low-crowned teeth which must have been situated within the mouth cavity. The posterior sector of the premaxillary is not only covered with low-crowned, close-set teeth on the facial surface, but also it is shorter and narrower than in *Youngolepis*. In some specimens (e.g. V7240), the posterior end of the premaxillary is very thin. All this suggests that, unlike in *Youngolepis*, the entire posterior sector of the premaxillary not only lies inside the mouth cavity but is attenuated and possibly reduced. Consequently, the posterior nasal opening immediately lateral to the posterior sector of the premaxillary lies at the very margin of the mouth cavity.

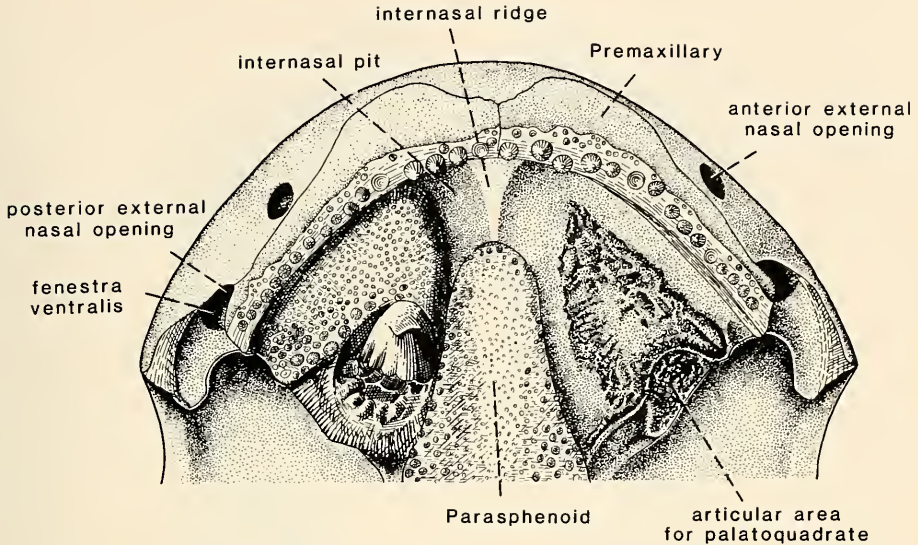


Fig. 3. *Youngolepis precursor* Chang et Yu. Snout in ventral view. Vomer on left side removed. After Chang, (1982).

So far no maxillary has been found and, except for the lower jaw tentatively allocated to this new form, there is no circumstantial evidence bearing on the presence or absence of this bone. Given the assumption that the maxillary did exist *and* that its anterior end connected with the posterior end of the premaxillary which lies inside the mouth cavity, one could infer that the anterior sector of the maxillary also lay inside the mouth cavity. However, the posterior sector of the premaxillary is so short, and its posterior end so thin and narrow in specimen V7240, that some interruption between the premaxillary and maxillary would not be inconceivable, even if the presence of the maxillary could be assumed.

Lateral to the opening in the posterolateral part of the floor of the nasal cavity, the ventrolateral part of the postnasal wall and the anterolateral wall of the nasal cavity manifest remarkable thickening. In the anterolateral part of the skull roof a long narrow overlapped area on the element probably corresponding to the lateral rostral and anterior tetal (i.e. prefrontal) of the osteichthyans, is visible from the ventral side. This area is probably overlapped by some plate traversed by the infraorbital sensory canal (cf. lachrymal of osteichthyans).

Judging from the prepared portions of the specimens, the endocranium is deep and narrow and the palatoquadrate is not fused with the endocranium. Lateral to the parasphenoid and ventral to the opening for the optic nerve, the ventral wall of the endocranium bears a well-delineated paired depression; there is no periosteal lining in the bottom of the depression and most probably it represents one of the areas where the palatoquadrate articulates with the endocranium. The basiptyergoid process occupies a fairly dorsal position. Passing through the dorsal wall of the nasal cavity in specimen V7241, are many tiny tubes, rather like the rostral tubuli found in fossil dipnoans (cf. Thomson and Campbell, 1971: 70, fig. 69; Miles, 1977: 129-132, figs 60, 63 etc.; Campbell and Barwick, 1984). These tiny tubes are also of the same nature as the network of fine canals in the endocranium of *Youngolepis* (Chang, 1982: 29, fig. 13) and *Powichthys* (Jessen, 1975: 219).

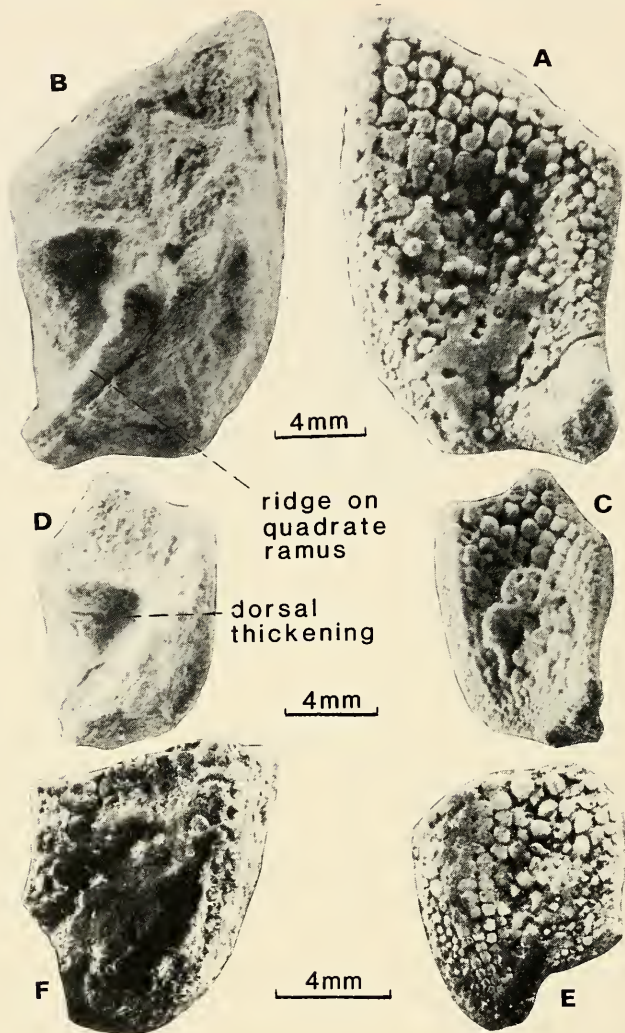


Fig. 4. *D. speratus* gen. et sp. nov. Left pterygoid in buccal (ventral) (A, C, E) and visceral (dorsal) (B, D) view, and right pterygoid in buccal view (F). A, B, specimen V7246; C, D, V7242; E, V7244; F, V7245.

Detached pterygoid plates: This material also includes some detached tooth bearing plates (Fig. 4). These plates are somewhat similar to those described by Denison, (1968a: 408, fig. 26) and detailed observations show that they can be identified as pterygoids (or endopterygoids). As can be seen in the well-preserved specimen V7246, such plates consist of a horizontal part and a ventrally curved quadrate ramus. In all the specimens so far found, the quadrate ramus is incomplete with its distal portion broken away. The horizontal plate has a medial margin which is slightly convex posteriorly, a straight lateral margin, and a slightly concave posterior margin. The entire buccal surface of both the horizontal plate and the proximal portion of the quadrate ramus, is covered by closely-set small teeth (Fig. 4A, C). These teeth are similar to those found on the premaxillary, the vomer and the parasphenoid. They are small in the posterior portion of the plate and larger on the anterior portion. These teeth appear to be arranged in regular rows and the spaces between the rows are taken up by much smaller teeth.

Some of the teeth on the posterior part of the plate are fused with each other in certain specimens (Fig. 4).

The visceral (dorsal) surface of the pterygoid (endopterygoid) has a marked lateral thickening and the quadrate ramus carries a high dorsal ridge (Fig. 4B, D). This is very similar to the normal structure of fossil dipnoans (e.g., *Dipterus*, *Chirodipterus*, *Holodipterus*; cf. Miles, 1977: 165, 168, 170, figs 76-77). Thus the configuration of these tooth-bearing plates, the tooth row arrangement pattern, and particularly the dorsal surface of these plates all correspond with dipnoan pterygoids (or endopterygoids), which bear typical tooth-plates in previously known forms. The only differences are that the teeth on the anterior part of the plate are not completely fused into tooth-plates and the quadrate ramus is covered by closely-set small teeth (at least in the proximal portion).

The allocation of these detached pterygoid plates to the present form, which is mainly represented by anterior cranial portions, is supported by the fact that the morphology of the teeth and the tooth-wear pattern are very similar to those found on the premaxillary, the vomer and the parasphenoid in more complete specimens. As the parasphenoid reaches the ventral part of the ethmoidal region anteriorly and adjoins the vomer, the pterygoid tooth-bearing plates cannot possibly meet in the midline.

Lower jaw: Our collection includes two right lower jaw rami, and an incomplete tooth-bearing portion from a left ramus. As is shown by a well-preserved right lower jaw ramus (specimen V7247, see Fig. 5), the main tooth-bearing portion is probably formed by the prearticular, or by the fused elements of prearticular and coronoid. The teeth have a fan-shaped or radiate arrangement and are similar to the lower jaw plate in *Dipterus valenciennesi* (Jarvik, 1967: 172, text-fig. 6). Most probably this portion occluded with the tooth-bearing pterygoid plate described above. Anterolateral to this main tooth-bearing part, there is a small portion formed by the inward bending of the dentary. This portion is also covered with small teeth and the tooth band thus formed

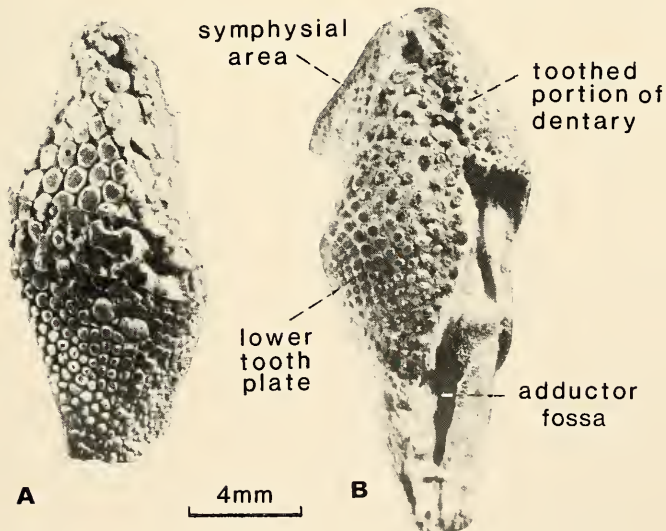


Fig. 5. *D. speratus* gen. et sp. nov. Right lower jaw ramus (A) and left lower jaw tooth-bearing portion (B). A, specimen V7247; B, V7249.

probably occluded with the tooth band formed by the premaxillary and the vomerine teeth lying near the mouth margin in the roof of the mouth cavity. No lateral toothed structure lies posterior to this portion, a point reinforcing the view that no toothed maxillary was present. However, such inferences depend on the validity of the assumption that the lower jaw belongs to the same species as the crania and the detached pterygoid plates.

The adductor fossa in the lower jaw reveals no considerable differences from the condition in previously known dipnoans, and the symphyseal area between the right and left rami is fairly broad (Fig. 5). The dermal bones on the external side of the lower jaw can be identified by complete or incomplete sutures. In specimen V7248, the dentary, splenial, postsplenial-angular and surangular bones, as well as openings of the mandibular sensory canal can be observed.

DISCUSSION

Position of Diabolichthys in relation to dipnoans: Comparison of cranial features among osteichthyans shows that this new form shares the following unique features with previously described dipnoans rather than with 'crossopterygians' or actinopterygians:

1). The bone series on the skull roof carrying the anterior and middle/posterior pit-lines are separated or partly separated by a median bone, and do not meet their antimeres in the midline. This is similar to the topographical relationship of I, J and B-bones uniquely found in dipnoans, the pattern being specially close to that found in primitive dipnoans such as *Dipnorhynchus* and *Uranolophus*.

2). Corresponding to the downward and inward bending of the snout, a considerable portion of the premaxillary lies inside the mouth cavity and its posterior sector is attenuated and possibly reduced. Moreover, the anterior and posterior external nasal openings occupy a ventral position and lie at the margin of the mouth cavity.

3). The pattern of palatal dermal bones and that of the dermal bones on the lingual side of the lower jaw, together with the tooth pattern of these bones and of the premaxillary, suggest that *Diabolichthys* had developed a palatal bite, which is found in all previously described lungfishes.

4). The anterior portion of the skull roof carrying the supraorbital sensory canal and the anterior pitline (cf. anterior shield, Miles, 1977; fronto-ethmoidal shield, Jarvik, 1942, 1980) is long while the posterior portion with the middle/posterior pit-lines (cf. posterior shield, Miles, 1977; parietal shield, Jarvik, 1942, 1980) is relatively short. The anterior portion in relation to the posterior portion is longer in *Diabolichthys* than in all non-dipnoan osteichthyans, though still not as long as in previously-described dipnoans.

However, as *Diabolichthys* also reveals remarkable differences from previously-described dipnoans (the palatoquadrate not fused with the endocranium and the pterygoids not meeting in the midline due to the forward extension of the parasphenoid to the ethmoidal region), it would be difficult to decide if this new form is a dipnoan without agreement on which characters are necessary and sufficient to define that group. Comparison of previous works involving dipnoan phylogenies (e.g., Bertmar, 1968; Thomson and Campbell, 1971; Miles, 1977; Rosen *et al.*, 1981) suggests that it would be more informative to regard *Diabolichthys* as more closely related to dipnoans than to other osteichthyans, and to conclude that the genus constitutes the sister-group of all previously described dipnoans (cf. Miles, 1977: fig. 157).

Consistent with the above position of *Diabolichthys* are other characters where this form agrees with primitive dipnoans such as *Dipnorhynchus* and *Uranolophus* and differs from later lungfishes. These include such features as the I-bones meeting posteriorly,

the orbit anteriorly positioned, the length of the I-bone and the lateral series corresponding to Y_1 , Y_2 and X-bone series, and the long parasphenoid (cf. Lehmann and Westoll, 1952: 410, figs 1B, 4B, pl. 24B; Denison, 1968: 372, fig. 8).

Problems in placing Diabolichthys in a more general phylogenetic scheme: On the basis of present knowledge of the relevant groups, the position of *Diabolichthys* as the sister-group of previously-described dipnoans is not seriously weakened by any characters uniquely shared by *Diabolichthys* and non-dipnoan osteichthyans. Similarities observed between *Diabolichthys* and other forms, including the associated 'crossopterygian' *Youngolepis*, could be parsimoniously regarded as symplesiomorphies (i.e. more general resemblances defining a more inclusive taxon). Chang (1982) briefly discussed the possible relationship of *Youngolepis*, and she cited several uniquely-shared characters suggesting that *Youngolepis* is more closely related to *Powichthys* (Jessen, 1975, 1980) than to any other forms. Although some of the characters she cited could now be interpreted as primitive features in the light of characters revealed by *Diabolichthys*, the sister-group relationship of *Youngolepis* and *Powichthys* is not challenged by any competing alternatives. There is no character uniquely shared by *Youngolepis* and *Diabolichthys*, while the only character possibly linking *Diabolichthys* and *Youngolepis/Powichthys* (i.e. independent premaxillary and sutural position of anterior section of the infraorbital sensory canal and the ethmoidal commissural canal) is invalidated by its presence in actinistians, and by its variability within taxa.

Given the hypothesized sister-group relationship between *Youngolepis* and *Powichthys*, and that between *Diabolichthys* and previously known dipnoans, it would be possible to define a more extensive group, with *Youngolepis-Powichthys* as the sister-group of *Diabolichthys*-plus-previously-described-dipnoans. This more extensive group is linked by at least one character so far not reported in any other forms (i.e. the presence of rostral tubuli forming a network of fine canals in the endoskeletal part of the snout; cf. Jessen, 1975; Chang and Yu, 1981; Chang, 1982; Miles, 1977; Thomson and Campbell, 1971). The characters associated with the degree of downward bending of the snout and the relatively ventral position of the anterior and posterior nasal openings are basically consistent with this scheme, although the significance of these characters is somewhat dependent on associated notions about the modification of the snout and the nasal openings in the relevant groups.

Attempts to determine the position of *Diabolichthys* in relation to 'rhipidistians', actinistians, and tetrapods are complicated by many unresolved problems (cf. Rosen *et al.*, 1981: figs 4 and 62). In particular 'rhipidistians' make a poorly-defined group, and it is difficult, if not impossible, to determine their relationships with any new group, as was well shown by the study of *Youngolepis* and *Powichthys* (but see Jessen, 1980). However, since no characters have been found which uniquely link 'rhipidistians' or their subgroups with *Youngolepis-Powichthys*, or with *Diabolichthys*-plus-previously-known-dipnoans, the sister-group relationship between *Youngolepis-Powichthys* and *Diabolichthys*-plus-previously-described-dipnoans is not weakened by the probable paraphyletic nature of 'rhipidistians'. It is the intuitive feeling of the present authors that when 'rhipidistians' are divided into monophyletic taxa at various levels, most of them will occupy a range of positions plesiomorphous to that of *Youngolepis-Powichthys* and *Diabolichthys*-plus-previously-described-dipnoans. The present discussion omits consideration of the position of actinistians and tetrapods, an issue that we regard as intractable at present. Our view that 'rhipidistians' occupy a range of plesiomorphous positions in relation to *Youngolepis-Powichthys* and *Diabolichthys*-plus-previously-described-dipnoans does not imply any preconceived notion on the relations between tetrapods, 'rhipidistians' and dipnoans, though the phylogenetic scheme of the present paper could be considered as generally more consistent with some of the competing

hypotheses involving sarcopterygians and tetrapods and less consistent with others (cf. Rosen *et al.*, 1981: figs 4, 62).

Comment on the choana problem in the light of Diabolichthys: Previous phylogenetic schemes linking tetrapods with 'rhipidistians' (e.g. Jarvik, 1942, 1972, 1980; Thomson, 1964; Miles, 1977) or with dipnoans (Rosen *et al.*, 1981) depend heavily on the interpreted presence or absence of a choana in 'rhipidistians' and dipnoans. Jarvik and others held that: 1) tetrapods and 'rhipidistians' have a choana as a new formation not homologous with the posterior nasal opening of fishes, whereas the lachrymal duct, supposed to exist in 'rhipidistians' as well as tetrapods, is the homologue of the posterior nasal opening of fishes in general; 2) with the interpreted choana in tetrapods and 'rhipidistians', the premaxillary-maxillary arcade exists in these forms with no interruption; and 3) the palatal opening in dipnoans is the posterior excurrent nasal opening that has migrated onto the roof of the mouth cavity, and this opening lies lateral to the premaxillary-maxillary arcade, which has been subsequently reduced together with the anterior sector of the infraorbital sensory canal. On the other hand, Rosen *et al.* (1981) suggested that: 1) the tetrapod choana is homologous with the posterior nasal opening in fishes, and thus also with the palatal opening in dipnoans, whereas the tetrapod lachrymal duct is homologous with the labial cavity in dipnoans, a structure not found in other fishes; 2) the premaxillary-maxillary arcade exists in tetrapods, 'rhipidistians' and dipnoans; and with the posterior nasal opening assuming a ventral position in the roof of the mouth cavity of tetrapods and dipnoans, the premaxillary-maxillary arcade was interrupted in these two groups. The posterior nasal opening (interpreted as a choana) lies medial to the premaxillary-maxillary arcade both in tetrapods and dipnoans; 3) 'rhipidistians' probably have no palatal nasal opening (i.e. no choana) either as a new formation or as a modified posterior nasal opening.

Given the suggested position of *Diabolichthys* as the sister-group of previously-described dipnoans, it is natural to consider the relation between the premaxillary-maxillary arcade and the position of the posterior nasal opening in this form. Its anterior and posterior nasal openings are situated at the very margin of the mouth cavity, but the posterior one is lateral and not medial to the premaxillary. The attenuated and possibly reduced posterior sector of the premaxillary in *Diabolichthys*, and the evidence of detached lower jaw material allocated to this form, suggest either the absence of a toothed maxillary, or alternatively an interruption between the premaxillary and maxillary (see previous descriptive sections). Without considering the second alternative, the condition in *Diabolichthys* with the posterior nasal opening at the mouth margin but lateral to the premaxillary, might be considered as inconsistent with Rosen *et al.*'s interpretation of the dipnoan condition. However, the possible interruption of the premaxillary-maxillary arcade in *Diabolichthys*, the snout morphology of the genus, and its assumed phylogenetic position, could suggest an alternative scenario in which the posterior nasal opening moved to a ventral position inside the mouth cavity through the gap in the interrupted premaxillary-maxillary arcade. This scenario would not exclude the existence of an *interrupted* premaxillary-maxillary arcade *lateral* to the posterior excurrent nasal opening in dipnoans, and could suggest a possible solution to the dilemma in which one must either quote the existence of the premaxillary-maxillary arcade *lateral* to the posterior excurrent nasal opening, or invoke the total disappearance of this arcade *medial* to the said opening, in order to accept or reject the homology of the dipnoan posterior nasal opening with the tetrapod choana. With the adoption of a ventral position for the posterior nasal opening, and the transition from a marginal to a palatal bite as hypothesized by many authors, the elements of the *interrupted* premaxillary-maxillary arcade could have been modified, and/or fused with

other elements, and this could have been the case with *Griphognathus whitei*, as suggested by Rosen *et al.* (1981). The homology or non-homology of the tetrapod choana and the posterior excurrent nasal opening in dipnoans depends primarily on the question of whether the tetrapod choana is homologous with the posterior nasal opening in fishes in general. The latter question depends in turn on the problem of the structure of this region in 'rhipidistians', i.e. whether these forms possess a palatal nasal opening and, if they do, whether this opening co-exists (i.e. is non-homologous) with the posterior nasal opening or a structure which is unquestionably modified from it.

Since Rosen *et al.*'s (1981) analysis was presented, Chang (1982) has described the condition in *Youngolepis*, in which the ventral fenestra of the nasal capsule has no exoskeletal opening into the mouth cavity, and the only outlet is through the posterior external nasal opening. On this basis, the existence of a choana in *Powichthys*, as assumed by Jessen (1975, 1980) was questioned, and variations in the position of the opening in the post-nasal wall of *Euthenopteron foordi* were noted, bringing into doubt the interpreted homology of this opening with the lachrymal duct (or the posterior nasal opening according to Jarvik, 1942). On the basis of personal observations Chang also considers the reported choana in *Porolepis* and *Glyptolepis* as highly speculative, and not supported by morphological details. However, many of the relevant features in the various taxa referred to as 'rhipidistians' are far from clear, and a reasonable solution of the choana problem will require future research in many different quarters.

CONCLUSIONS

1. Analysis of character distribution suggests that *Diabolichthys* is more closely related to dipnoans than to any other osteichthyans and that it constitutes the sister-group of all previously-described dipnoans. In a broader phylogenetic scheme, *Youngolepis-Powichthys* forms the sister-group of *Diabolichthys*-plus-previously-described-dipnoans. However, the hypothesized relationship between the above group and 'rhipidistians' is constrained by the inherent difficulties in choosing between the different phylogenetic schemes of sarcopterygians.

2. Morphological features revealed by *Diabolichthys*, such as the skull roof pattern, palatal and lower jaw structures in relation to the palatal bite, and features associated with the downward and inward bending of the snout, might have significance for current debates on the interrelationships of lobe-finned fishes.

3. In *Diabolichthys*, the posterior nasal opening lies at the mouth margin but lateral to the premaxillary. The attenuated and possibly reduced posterior end of the premaxillary and the condition of the lower jaw, suggest that this form either lacked a toothed maxillary or that there was an interruption between the premaxillary and maxillary. With the assumed interruption in the premaxillary — maxillary arcade, it is possible to suggest an alternative scenario about the snout modification leading towards the dipnoan condition.

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References

- BERTMAR, G., 1968. — Lungfish phylogeny. *Nobel Symposium* 4: 259-283.
- CAMPBELL, K. S. W., and BARWICK, R. E., 1984. — The choana, maxillae, premaxillae and anterior palatal bones of early dipnoans. *Proc. Linn. Soc. N.S.W.* 107: 147-170.
- CHANG, M. M., 1982. — *The braincase of Youngolepis, a Lower Devonian crossopterygian from Yunnan, southwestern China*. Stockholm: GOTAB. 113pp.
- , and YU, X. B., 1981. — A new crossopterygian, *Youngolepis precursor*, gen. et sp. nov., from Lower Devonian of E. Yunnan, China. *Scientia Sinica* 24: 89-97.
- DENISON, R. H., 1968. — The evolutionary significance of the earliest known lungfish *Uranolophus*. In 'Current problems of lower vertebrate phylogeny' (ed. T. ØRVIG), *Nobel Symposium* 4: 247-257. Stockholm: Almqvist and Wiksell.
- , 1968a. — Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana (Geol.)* 17(4): 353-431.
- JARVIK, E., 1942. — On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zool. Bidrag fran Uppsala* 21:235-675.
- , 1966. — Remarks on the structure of the snout in *Megalichthys* and certain other rhipidistid crossopterygians. *Arkiv Zool.* 19(2): 41-98.
- , 1967. — On the structure of the lower jaw in Dipnoans: with a description of an early Devonian dipnoan from Canada *Melanognathus canadensis* gen. et sp. nov. In 'Fossil vertebrates' (eds C. PATTERSON and P. H. GREENWOOD). *J. Linn. Soc. London (Zool.)* 47: 155-183. London: Academic Press.
- , 1972. — Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. and a discussion on the structure of the head in the Porolepiformes. *Meddel. Grønland* 187(2): 307 pp.
- , 1980. — *Basic structure and evolution of vertebrates*. London: Academic Press.
- JESSEN, H., 1975. — A new choanate fish, *Powichthys thorsteinssoni* n. g., n. sp., from the early Lower Devonian of the Canadian Arctic Archipelago. *Colloques int. Cent. natn. Rech.* 218: 214-222.
- , 1980. — Lower Devonian Porolepiformes from the Canadian Arctic with special reference to *Powichthys thorsteinssoni* Jessen. *Palaeontographica (A)* 167: 180-214.
- LEHMANN, W. M., 1956. — L'évolution des Dipneustes et l'origine des Urodeles. *Colloques int. Cent. natn. Rech. scient.* 60: 69-76.
- , and WESTOLL, T. S., 1952. — A primitive dipnoan fish from the Lower Devonian of Germany. *Proc. Roy. Soc. London.* B140: 403-421.
- LI, X. X., and CAI, C. Y., 1978. — A type-section of Lower Devonian strata in southwest China with brief notes on the succession and correlation of its plant assemblages. *Acta Geol. Sinica* 1978: 1-14. (In Chinese with English summary.)
- LIU, H. T., and YEH, S. K., 1957. — Two new species of *Ceratodus* from Szechuan, China. *Vertebrata Palasiatica* 1(4): 305-311. (In Chinese with English summary.)
- MILES, R. S., 1977. — Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *J. Linn. Soc. London (Zool.)* 61: 1-328.
- ROSEN, D. E., FOREY, P. L., GARDINER, B. F., and PATTERSON, C., 1981. — Lungfishes, tetrapods, palaeontology and plesiomorphy. *Bull. Am. Mus. nat. Hist.* 167: 163-275.
- THOMSON, K. S., 1964. — The comparative anatomy of the snout in rhipidistian fishes. *Bull. Mus. Comp. Zool.*, 131: 313-357.
- , and CAMPBELL, K. S. W., 1971. — The structure and relationships of the primitive Devonian lungfish — *Dipnorhynchus sussmilchi* (Etheridge). *Bull. Peabody Mus. nat. Hist.* 38: 1-109.
- WANG, J. Q., 1981. — A tooth plate of dipnoan from Qujing, Yunnan. *Vertebrata Palasiatica* 19(3): 197-199. (In Chinese with English summary.)